

The behavior and relationships of the Least Grebe

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ABSTRACT.—The Least Grebe, *Tachybaptus dominicus*, is widely distributed in the warm parts of the New World. It feeds on a wide variety of animals, including dragonflies and ants, the latter taken from emergent vegetation. Reverse mounting and copulation were filmed and analyzed. The former differed from the latter in that there was no cloacal contact and the series of post-mounting displays was less regular in timing and in alternation between members of the pair. The posture of the head in inviting differed from that of other grebes. No rearing or wing-quivering was observed. Four calls are described and the contexts in which they were used are discussed. The Least Grebe resembles the Old World little grebes, *Tachybaptus ruficollis* and *T. novaehollandiae*, in its cryptic resting posture, duet trills, and general habits; and it is probably more closely related to them than to any other grebes.

RESUMEN.—El zambullidor chico, *Tachybaptus dominicus*, tiene una distribución difusa sobre las partes calurosas del Nuevo Mundo. La comida de este zambullidor consiste de una variedad extensiva de animales, incluyendo libélulas y hormigas, éstas siendo cogidas de la vegetación emergente. El montaje reverso y la copulación fueron filmados y analizados. Aquél fue distinguido del éste en que no hubo contacto cloacal y los despliegos después del montar fueron menos regulares en duración y en alternación entre los miembros de la pareja. La postura de la cabeza en invitando no es como lo que se observa en los otros zambullidores. Ni la levantadura ni el estremecimiento de las alas fueron observados. Cuatro llamadas son descritas, y el contexto en que fueron usadas es discutido. El zambullidor chico es parecido a los zambullidores pequeños del Mundo Antiguo (*Tachybaptus ruficollis* y *T. novaehollandiae*) en su postura secreto de descanso, trino duo, y en hábitos generales; y es probable que es más estrechamente emparentado con ellos que con los otros zambullidores.

The Least Grebe (*Tachybaptus dominicus*) has a wide range, from the Greater Antilles and southern Texas south to northern Argentina. (Early records from central and southern Argentina are probably erroneous, Storer, 1975.) Birds of this species take wing more readily than most grebes and have a high reproductive potential (Gross, 1949); they are thus thought to be adapted for utilizing temporary ponds (Smithe and Paynter, 1963). On the other hand, the northern population is not migratory; in southern Texas many of these birds are killed in cold winters when the ponds on which they live are frozen (James, 1963). Least Grebes are found on still waters in the tropical and subtropical zones. In some areas, for example Costa Rica, they are said to be more numerous in the latter zone (Carriker, 1910; Slud, 1964). Not infrequently specimens have been taken as high as 6000 feet elevation; the highest elevation from which I have seen specimens is "about 9000 feet" at La Lejia, north of Chachapoyas, Peru (American Museum of Natural History Nos. 234,318; 234;319). The species has also been taken at 2500m elevation in Bolivia (Carnegie Museum No. 120,163, from Comarapa, Dept. Santa Cruz).

In spite of the species' wide range, little is known about its biology. Much of the meagre literature is summarized in Palmer (1962), but even there one finds little on courtship, nothing on mating behavior or thermoregulation; and food habits are based on the examination of but ten stomachs. In order to learn more about this species, I made two trips to southern Texas, from 21 March to 4 April and from 24 April to 4 May, 1971. Most observations were made with the aid of 9 X binoculars, behavior was filmed with a 16 mm Bolex motion picture camera, and vocalizations were recorded with a Uher tape recorder. The field work was done primarily at the Santa Ana National Wildlife Refuge and at Anzalduas State Park, both in Hidalgo Co. This was supplemented by observations made at the Rob and Bessie Welder Wildlife Foundation near Sinton, San Patricio Co., and at a pond near Hargill, Hidalgo Co. Additional information was gained from examining and measuring over 700 specimens of the species from 24 collections in the United States and

Canada. Analysis of geographic variation will be presented in a later paper. I am especially indebted to Robert W. Dickerman for specimens, Joseph G. Strauch, Jr., and Thomas E. Moore for stomach analyses, Daniel H. Janzen for identifying ants and for information on their habits, L. K. Gloyd for help identifying dragonflies, Gene Blacklock, the late Clarence Cottam, Pauline James, Albert McGrew, and Wayne A. Schifflett for their assistance with the field work, Patricia J. Wynne for preparing the illustrations, Rafael Alvarez for translating the abstract, to the National Science Foundation (through Grant GB-8269) for financing the study, and to the curators of the collections studied for making their material available. The kindness and hospitality of these people have made the work a great pleasure.

The Least Grebe is appropriately named. The mean weights of 18 males and 18 females from North and Central America are 140 g and 123 g, respectively. Birds of the Greater Antillean population are somewhat heavier (mean weight of four males, 167 g) and those of the South American population somewhat lighter (mean weight of three males, 114 g). The Least Grebe's ecological counterpart in much of the Old World, the Little Grebe (*T. ruficollis*), is somewhat larger: mean weights of six males and six females from East Africa are 180 and 152 and for 187 winter-taken birds from Germany, not segregated by sex, 192 g (Hölzinger and Schilhansl, 1968). Philippine birds are still larger.

The Least Grebe is one of the drabest members of the family with less difference between winter and nuptial plumages than most grebes. In nuptial plumage, the chin and throat are black and those parts of the plumage which are below the waterline when the bird is swimming are heavily marked with sooty. In winter, the chin, throat, and underparts are white. In contrast with the widespread Old World little grebes (*T. ruficollis* and *T. novaehollandiae*) there is no bright patch at the gape during the breeding season. Instead, the eye is bright yellow or orange in breeding Least Grebes. As is usual in grebes, the remiges are shed simultaneously, but the timing of this molt appears to be irregular. I have examined seven specimens from Texas with new remiges which had not completed growth. These birds were taken in August (1), September (2), January (2), March (1), and May (1). It is clear that the timing of the molt in this species merits further study.

These birds often gather in small flocks outside the breeding season, when they also associate with other species of water birds. When breeding, they are territorial but may nest in loose aggregations. Predation by Bat Falcons (*Falco ruficularis*) has been reported by Dickey and van Rossem (1938). A possible means of accidental death is indicated by data on a specimen of Least Grebe in the University of Michigan Museum of Zoology, collected on the Laguna de Sotz, Petén, Guatemala, by C. L. Hubbs. This bird had climbed onto a waterlily leaf, the center of which sank with the bird's weight and formed a funnel which trapped it.

Least Grebes move very quickly compared with larger species. This is quite noticeable in their comfort movements, which are in general similar to those of other grebes. I observed bathing, preening, oiling, head-shakes, head-scratches, jaw-stretches, foot-shakes, wing-and-leg-stretches, two-wing-stretches, swimming-shakes, and wing-flaps (the last two especially rapid). Bathing was particularly vigorous, the birds sending up a spray two to three feet high. I could detect no lateral motion of the tail as in swimming-shakes of Anatidae (McKinney, 1965). In both-wings-stretches, Least Grebes raise and partially stretch out their wings to a position intermediate between that of the Horned Grebe (*Podiceps auritus*) and that of most other species (Storer, 1969).

Miller (1932) and Wetmore (1965) comment on the flying ability of Least Grebes, and I agree that they probably take wing more readily than other North American grebes. They frequently flutter across the surface in the course of aggressive encounters or when frightened. I also saw what I believed was an upwind flight, when a bird flew low over the water against the wind, apparently to keep away from

the lee side of a pond. (The habit of resting in clumps of emergent vegetation may also be a means of keeping from being blown to shore.) I saw several flights in which the birds went higher (to 5 or 6 ft. above the water) but could not see other birds which might have been involved in triggering this behavior. I saw no flights which I could attribute to courtship behavior (cf. Palmer, 1962).

The resting or "pork-pie" posture of the Least Grebe is like that of other grebes in that the head is held forward beside the neck, but it differs from the comparable posture of larger species in that the scapulars, and probably also the inner secondaries, are raised like a tent, hiding the nape and sides of the head (Fig. 1D). Birds in this posture show little or no white and appear more like a small stump than a bird. This unbirdlike form probably has survival value in permitting the birds to escape notice of visual predators. The resting posture of the Little Grebe (Bandorf, 1970: 19, fig. 5) resembles that of the Least Grebe very closely.

Food and foraging.—The feeding habits of the Least Grebe are poorly known. Stomach contents and feeding habits have been reported by Bond (1934), Cottam and Knappen (1939), Friedmann and Smith (1950), Gross (1949), and Wetmore (1965). According to these reports, the food taken includes aquatic beetles and true bugs, dragonfly and damselfly nymphs and adults, shrimp-like crustaceans, crayfish, small fishes, and tadpoles. (The decayed vegetable matter, algae, and mud reported as food of this species by Gross, 1949, and filamentous green alga (*Chara*) found in the Least Grebe stomach by Bond, 1934, may have been ingested accidentally with their usual animal food.) To the analyses of the nine stomachs mentioned in the above references, I have been able to add data from eight birds collected by Robert W. Dickerman in Mexico and Guatemala and examined by J. G. Strauch, Jr. The results of these analyses are presented in the appendix.

As suggested by the variety of foods taken, Least Grebes use a variety of foraging techniques. I saw them forage not only by the usual grebe method of diving, but also by immersing only the head and neck, by picking objects off the surface of the water and off emergent vegetation, and by snapping at passing insects. I have observed all these methods but the last in at least one other species of grebe, and the last has been reported for the Great Crested Grebe (*Podiceps cristatus*) by Chance (1970) and Crow (1951). Once I saw a female Least Grebe stop preening to dash after a mating pair of dragonflies, apparently catching them as they came to the surface of the water. She ate first one and then the other, which meanwhile had lain immobilized on the water. Each was larger in body size than the bird's bill. Another time, I saw a Least Grebe, which had been sunning, start swimming rapidly with its head forward and wings down after a fairly large, red-bodied dragonfly with red on the wings (probably *Libellula (Belonia) saturata*, fide L. K. Gloyd). The grebe snapped at the dragonfly as it flew over, but missed. Shortly the bird dived and emerged, snapping at the insect as the latter came near the surface. This trout-like foraging method is one which I have never seen performed by any other bird. The largest dragonfly which I saw a Least Grebe eat was perhaps 4 inches long (possibly an *Anax*). After catching it, the bird swam rapidly away from the nearby grebes and eventually swallowed the insect headfirst, wings and all. As is the case with other grebes, large prey are shaken and pinched with the bill before being swallowed.

On March 23, at Welder, I watched six Pied-billed Grebes (*Podilymbus podiceps*) and two Least Grebes diving and feeding together among the roots of a patch of *Scirpus*. At times they were almost touching. They were getting small, whitish objects (shrimp or small fishes) about $\frac{3}{4}$ inch long. The lack of antagonism was strikingly different from the situation later in the spring at Santa Ana Refuge when the Pied-billed Grebes were nesting. Commensal feeding of Least Grebes with domestic Mallards and Horned Grebes with a Surf Scoter have been reported by Paulson (1969). Feeding associations between Little Grebes (*Tachybaptus ruficollis*) and ducks and coots have been reported by several observers and summarized by

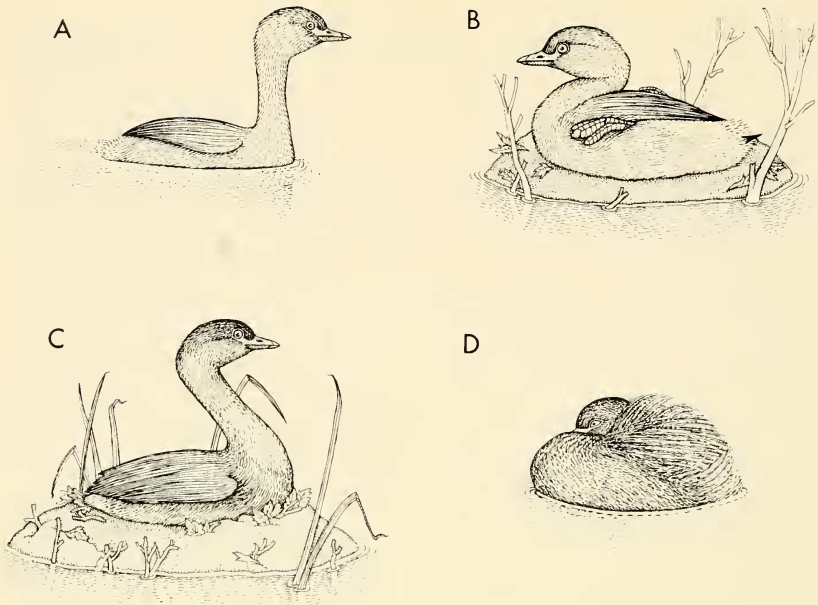


Figure 1. Postures of the Least Grebe. A. Alert posture. B. Resting on nest with feet held out. C. Z-neck posture on nest. D. Pork-pie resting posture.

Siegfried (1971). The association between the two species of grebes differed from those between Little Grebes and unrelated species in that the two grebes apparently used the same foraging techniques and ate the same food.

Other food items which I saw brought to the surface were a fish less than an inch long, and a somewhat smaller tadpole. My observations are probably biased in favor of large prey items, for, like Horned Grebes (Storer, 1969), Least Grebes probably swallow small prey items before surfacing. This is further indicated by the stomach analyses. However, it is evident that dragonflies are a much sought-after prey.

The occurrence of ants in seven of the eight stomachs and their presence in large numbers in two deserves special comment. Daniel H. Janzen looked at samples of these ants and identified most as belonging to the genus *Crematogaster* and others to the genera *Pseudomyrmex* and *Camponotus*. According to him, members of these three genera nest in hollow twigs, dead branches, or stumps and but rarely in the ground. Thus they may be found in numbers in dead bushes or trees standing in bodies of water, which are either temporary or have wide seasonal fluctuations in size. Many of the head capsules were crushed, so it is likely that most of the ants were taken one by one from emergent vegetation.

Least Grebes are thus opportunistic feeders, taking a variety of small animals both in and on the water, in the air, and on emergent vegetation. This flexibility in foraging and in particular taking many terrestrial insects which either land on the surface or are found on emergent vegetation probably enables them to use temporary bodies of water, where invertebrate populations may be unstable or transitory.

Cottam and Knappen (1939) commented on the small volume of feathers in the stomachs of Least Grebes which they examined. Of the eight stomachs which we

analyzed, four had few feathers, two had many, and two moderate numbers. In at least three, there was a plug in the pyloric lobe similar to that which I reported for the Horned Grebe (1969). Such a plug was present in each of six stomachs of the Pied-billed Grebes examined recently and may prove to be the rule in all species of the family. The paucity of feathers in so many of these stomachs can, I believe, be explained by the high proportion of insects in the diet and the consequent need for frequent pellet casting to get rid of indigestible chitin.

Agonistic behavior.—Like most or all others of their family, Least Grebes meet in breast-to-breast combat, kicking out at each other like coots. Because of the great strength of the shank muscles, which power the swimming strokes of the feet, the comparable downstroke in fighting is presumably the one used to the greatest effect. At least seven such fights were observed, the earliest on March 27 and the latest on May 3. The birds involved were, as far as I could tell, all males, some with white throats and some with black or pied throats.

Chases were frequent, one bird skittering across the water after another, both moving their wings and feet rapidly. On one occasion an apparently mated male dived and chased an odd male, who made three zig-zag skitters, each six to eight feet in length, while the aggressor underwater evidently followed its path. The aggressor emerged in a posture like that used in bathing (but here apparently of aggressive significance) before returning to his mate. This bathing posture was not unlike the bouncy posture used by species of *Podiceps* in the discovery ceremony (Storer, 1969) and might be an evolutionary source of this courtship display.

The most frequently noted threat posture was one in which the head was held high and somewhat back, the head, neck, and body forming a Z, and the head and neck feathers raised (Fig. 1C). This posture closely resembled the "bridling dog display" of the Atilán Grebe (*Podilymbus gigas*) figured by LaBastille (1974: fig. 11) and the similar display of the Pied-billed Grebe which I have seen on several occasions. That these displays are probably homologous is suggested by an observation of two male Least Grebes using the Z posture with the feathers raised in an aggressive encounter, presumably near the boundary of their territories. I saw a Least Grebe, which had just fled from another, assume a similar posture, but with the head and neck feathers flattened. This posture resembled closely the appeasing z-neck posture of the Horned Grebe (Storer, 1969) and probably had a similar appeasing motivation. An alert posture (Fig. 1A) was used when the birds were disturbed or appeared curious.

A stronger threat than the z-neck posture with the features raised is holding the head low as in the forward threat of other grebes. In still more aggressive situations, a Least Grebe may lunge, skitter, or dive toward a second bird. These actions are listed in what I believe to be their increasing intensity of threat. The similarity of the two z-neck postures in everything except the raising or lowering of the head and neck feathers suggests that both may have somewhat similar motivation. The head is held high in alarm and in advertising, both situations in which fear or anxiety is expressed; in strongly aggressive situations, the head is held low or forward. Thus there is probably a strong element of appeasement in both z-neck postures. Raising the feathers of the head and neck adds a balancing aggressive element, which may permit one bird to use this display against another bird using the same display on neutral ground.

Pied-billed Grebes were found on all waters where I observed Least Grebes. Early in the season, when the birds were in winter groups, individuals of both species foraged in close association. But at Santa Ana Refuge, after Pied-bills had mated and had started to nest, they were intolerant of Least Grebes. In late March and early April, two pairs of Pied-bills and up to eleven Least Grebes lived on the long, narrow, diked West Lake. The pair of Pied-bills established near the north end of the lake kept the Least in the south end by repeated aggression. Frequently a

Pied-bill would dive and move underwater toward one or a group of Least Grebes on the open water. This resulted in the Least skittering over the water, often into the cattails around the edge. After encounters with Pied-bills, Least Grebes often looked underwater and then raised their heads in an alarm posture. At times a Pied-bill would rout Least Grebes by swimming toward them in the flat-headed threat posture, whereas Least Grebes did not flee from Pied-bills in neutral postures. It was clear that the Least Grebes recognized the threat displays of the Pied-bills. In early May on the resaca at Anzalduas State Park where I photographed the mating behavior of Least Grebes, a male of this species near its nest twice threatened a Pied-bill, once with the z-neck aggressive posture, once by diving toward it. In both cases the Pied-bill moved away. Antagonism between these two species in Cuba has been described by Gross (1949) and LaBastille (1974) mentions a male Atitlán Grebe seizing a Least Grebe by the neck and thrashing it vigorously.

Thermoregulation.—Least Grebes sunbathe regularly, facing away from the sun and erecting the white feathers of the back. Solar energy is absorbed by the heavily pigmented bases of these feathers and by the black skin beneath them (Storer, Siegfried, and Kinahan, 1975). While on the nest platform, Least Grebes occasionally rested with the back feathers down and the spread toes held out from the body (Fig. 1B). The function of this behavior is unknown, but it may serve as a cooling mechanism.

Courtship.—It is not clear which courtship displays function in pair formation. I have observed neither the rushing display reported and figured by Zimmerman (1957) nor display flights like those described by Palmer (1962), which I could attribute to courtship. As in most other grebes, advertising is probably involved, but the other display or displays remain to be determined. Once pairs are formed, duetting trills upon meeting and after aggressive encounters with other grebes are probably important in strengthening the pair bond.

Platform behavior.—Between April 29 and May 3, I observed mating behavior of a pair of Least Grebes on a small resaca, 300 to 400 feet long and 75 to 100 feet wide on the east side of Anzalduas State Park. There were two pairs of Least Grebes and a pair of Pied-billed Grebes on this resaca, which contained considerable emergent vegetation, most of it dead shrubs. The pair which I spent most time watching had a platform in a dead shrub in full view from the slope leading down to the water. The members of this pair were readily distinguishable, the female by her shorter bill, more rounded, dove-like head, and completely black throat, and the male by his longer bill, flatter head, and white chin. When I first saw the platform, it was well built and easily supported the birds, who nevertheless added material, mostly algae, to it from time to time throughout the period of observation. When I left at 7 p.m. May 3, no eggs were as yet in it.

The pair bond appeared strong from the time of my first visit, and inviting was performed frequently by both birds. On April 30 and May 1, observation periods of approximately five and five and one half hours, respectively, inviting by the female was observed 8 and 10 times, and by the male, 7 and 7 times; mounting by the female 2 and 4 times, and by the male, 2 and 2 times. The female more frequently got onto the platform but tended to remain there for shorter periods than the male. In 13½ hours of observations on three days, the female was on the nest 31 times to the male's 21; but she remained there longer than 8 minutes only twice in 22 times (maximum 17 minutes), whereas the male remained longer than 8 minutes in 5 out of 15 observations (maximum, 25 minutes). This may well have been correlated with the female's spending more time away from the nest foraging during this period of development of the eggs, but foraging times could not be taken owing to the density of vegetation in the resaca.

On the basis of the single pair which I watched at their platform, Least Grebes differ from other species so far studied in their soliciting postures. I observed no

rearing or wing-quivering, and in the inviting posture the head was not extended but drawn back and the bill pointed downward at an angle of approximately 45° (Fig. 2D). This angle varied considerably, at times a bird would point the bill more downward at its mate's approach. The inviting bird also tended to turn its head away from its mate. Frequently when the mate was on the water beside or in front of the inviting bird, the latter would get up, turn, and settle down again in the inviting posture with the tail toward the mate. It has been suggested that rearing might be a ritualized intention movement of sitting down on the nest (McAllister, 1958), that it also resembles the posture of the active bird during copulation and that of a bird turning its eggs, and that it may be a "ritualized version of the waddling on the nest rim, shaking the wings to remove water from the plumage, and showing intentions to uncover the eggs, before settling to incubate (Schmidt, 1970, fide Fjelds , 1973). A fourth possibility is that rearing arose as a ritualization of a getting up and turning away from the mate like that performed by the Least Grebe.

An elaboration of the inviting posture was seen once, the female turning the head from facing forward to facing left to forward to right, etc., stopping briefly each time the head faced forward and at the extreme of each turn. During copulation, the female also turned her head in this way, gradually raising it until her nape stroked the breast of the male (Fig. 1A). A similar type of head turning was observed in the New Zealand Dabchick (*Poliiocephalus rufopectus*) (Storer, 1971) both in inviting and during copulation. Elaborations of this type of head turning are found in courtship displays of the latter species (Storer, 1971) and of the Great Grebe (*Podiceps major*) (Storer, 1963a).

Inviting in the Least Grebe is often accompanied by *gup* notes.

As in other grebes, mounting is preceded by a fairly long period during which the male remains on the water, moving about "nervously," as though getting up courage to mount. At this time, the male does not appear to perform any stereotyped movements. Mounting is not accompanied by loud calls, as is the case in most other grebes. After the male has mounted, he moves the tail from side to side (28 or 29 times in about six seconds in one film), then presses it against that of the female as cloacal contact is made. He then rises up a little and finally dismounts over the female's head. Upon hitting the water, he treads water rapidly as his body subsides onto it and his head is raised and held back in the z-neck posture. Water treading is done in front of and with one side toward the female, who remains on the nest.

While the male is treading water (Fig. 2C), the female initiates a series of post-copulatory displays. These include presumed calls (Fig. 2F), head flicks or shakes (Fig. 2D), and head turns. The first consists of opening the bill as though calling and lasts from four to seven frames with a mean of roughly one-fifth of a second. I noticed no sound, but one could easily have been unnoticed while the camera was running. Head flicks consist of two or three rapid sideways movements of the head and include a turning of the head approximately 45° on its long axis so that one side is turned partway up (cf. McKinney, 1965). Head shakes lack this turning on the long axis but are otherwise similar. Both are accomplished in approximately one-tenth of a second (2 or 3 frames of cin  film taken at 24 frames per second). Because of the speed of the actions it is likely that the turning may have been missed in some instances. For this reason and because I could see no significant difference in the use of the two displays, I have combined them under head flicks. Head turns are quick turns of the head in one direction, either toward or away from the mate. Turns also take approximately one tenth of a second, and their amplitude was estimated at 15° (once), 30° (19), 60° (29), and 90° (9 times). When the male turns his head, very often he subsequently turns his body slowly until its axis is parallel with that of his head. The female remains on the nest and turns only the head and neck. Between display movements, the birds hold their heads motionless as though posturing (Fig. 2E).

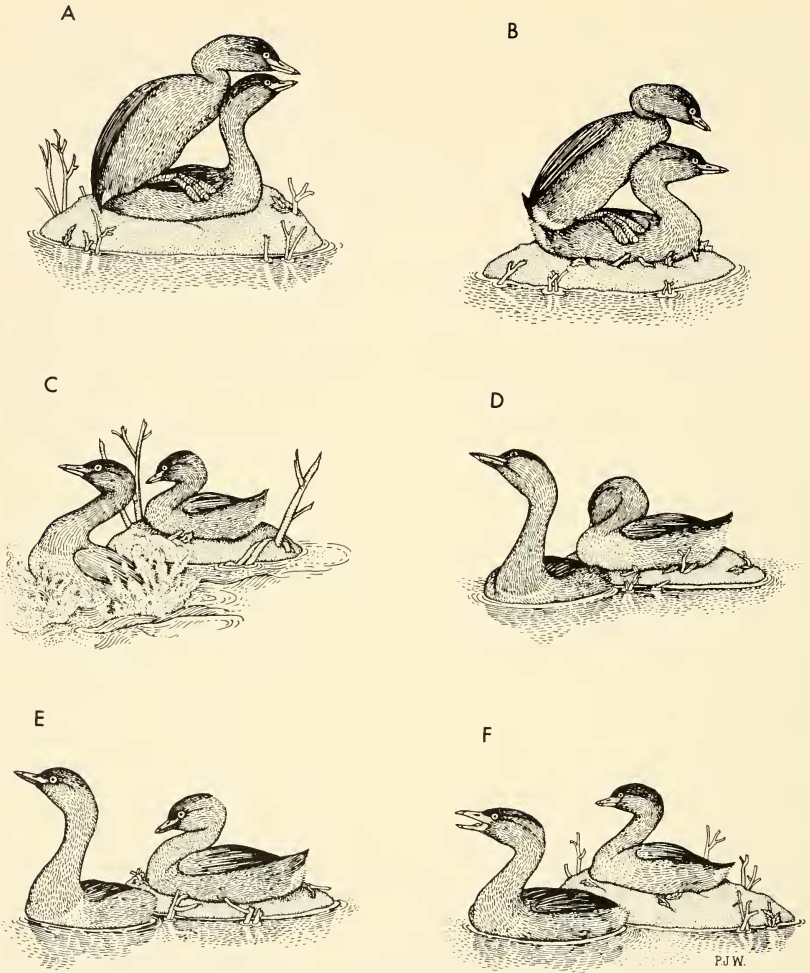


Figure 2. Platform behavior of the Least Grebe. A. Copulation. B. Reverse mounting. C. Water-treading. D. Head flicking by male, inviting by female. E. Posturing between head turns. F. Male calling.

The postcopulatory displays are performed alternately by the members of the pair. The female uses only head turns, except once when she gave a flick about one second (26 frames) after she gave a turn given while the male was water treading. This was also the only exception to the regular alternation between the sexes following copulation. The displays given by the male follow a general pattern—first a call, then one or more flicks (or shakes), and finally one or more turns. As the sequence of displays progresses, the intensity appears to wane until one or both birds move off. Thus by the position of the displays within the series one can postulate the relative intensities of the displays. Calls are presumed more intense than flicks, which are more intense than turns. The mean reaction time, that is, the interval between

TABLE 1. Reaction Times¹ between Postmounting Displays of the Least Grebe

	N	Mean	S.D.	S.E.
Male after copulation	11	15.6	8.15	2.45
Female after copulation	11	15.5	6.39	1.92
Male after reverse mounting	10	24.8	11.31	3.57
Female after reverse mounting	11	7.4	5.26	1.58

¹The number of frames of cine film between the start of a display by one bird and the succeeding display of its mate.

successive displays, was 15.6 frames and was the same for both sexes (Table 1). With a progressive decline in intensity of displays, one might expect a progressive increase in the intervals between displays. No such change was shown in the data; long and short intervals were found both early and late in the series. Nor was there evidence that the length of the interval was affected by whether the preceding motion of the head was toward or away from the responding bird.

Reverse mounting.—As mentioned earlier, reverse mounting (Fig. 2B) was observed more frequently than copulation. Although the two acts are superficially similar, studies of three copulation sequences and five sequences of reverse mounting with a film analyzer showed several significant differences. It was evident from the film that reverse mounting did not result in cloacal contact although the female did make side-to-side movements with the tail. The alternation of displays after copulation was more regular (in 23 of 24 displays) than after reverse mounting (in 23 of 33 displays, including one instance in which the female displayed three times in succession). After reverse mounting, there was a considerable difference between the sexes in the reaction time between displays, that of the male averaging more than three times that of the female (Table 1).

Reverse mounting has usually been dismissed without comment as aberrant or incidental behavior. In grebes it occurs frequently and probably regularly in most species. Hence, I believe that it must have a positive selective value to outweigh the rather obvious disadvantages of using energy which otherwise would be conserved or put to more direct reproductive effort and of drawing attention of potential predators to both the nest platform and the birds themselves. What the advantages are is unclear but worthy of speculation in the hope that further evidence or proof can be obtained. The lack of cloacal contact rules out fertilization. Some possibilities which remain include strengthening the pair bond, a change in dominance relationships, and providing a stimulus for the growth of the ovarian follicles or for ovulation.

Advertising call.—A loud, rather high-pitched note (Fig. 3), which I transcribed as *gamp*, apparently serves as an advertising call. In intense advertising, the note is given with the head held high and slightly puffed out, the neck thin, the white of the underparts showing above the water anteriorly, and the body feathers slicked down. This posture corresponds to that in advertising Horned Grebes (Storer, 1969: Fig. 3A), but it is not used in low-intensity advertising. The two pairs of Least Grebes at Anzalduas State Park, April 29 to May 3 gave this call or series of this call at least 40 times in approximately 11½ hours of observations. The call varied in intensity and was given under a variety of circumstances, but almost always when the members of a pair were separated and often when the calling bird was somewhat alarmed. (Only twice was I certain that a bird advertised when its mate was near; in each case it was the female which called and the calls were of low intensity.) Advertising calls were given by the male (14 times) and the female (4 times) when alone and undisturbed on or near the nest, in all but two of these instances the call was of low or moderate intensity. Twice when the male was at the nest calling, the female

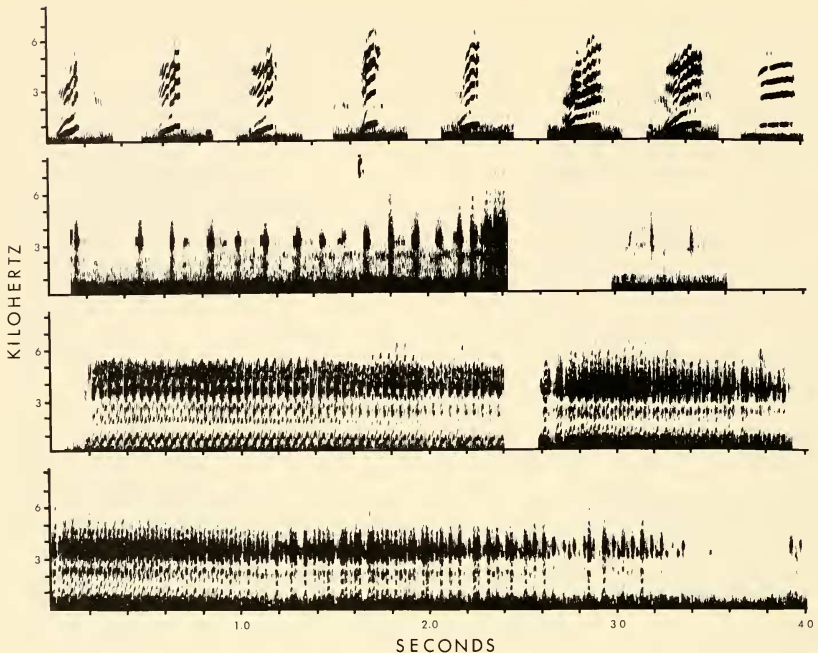


Figure 3. Vocalizations of the Least Grebe. *Top row*, advertising notes. *Second row, left*, start of trill, *right*, contact notes. *Third and fourth rows*, trills.

answered with similar advertising notes. Four times I disturbed lone birds (the male three times and the female once) on the nest, and they gave loud, high-intensity *gamps*. Other disturbances eliciting advertising calls included a splash, possibly made by a frog jumping into the water, and the presence of a Pied-billed Grebe or another pair of Least Grebes nearby.

Earlier at Santa Ana advertising notes were also heard.

While it is difficult to match verbal descriptions in the literature with calls heard in the field, I believe that the "reedy, somewhat nasal . . . *queek*" of Palmer (1962) and the "call which varies from a loud, goose-like honk to the reedy little honk of a toy horn" of Slud (1964) and the "nasal *yank* surprisingly similar to that of a red-breasted nuthatch" of Friedmann and Smith (1955) all refer to advertising calls.

Trills.—The most familiar and conspicuous call of this species is a loud, rapid trill, which is frequently heard when the members of a pair are together. Audiospectrograms (Fig. 3) indicate that at least part of the time both members of the pair call simultaneously, but with alternate notes. Trills may end abruptly or the tempo of the notes may slow down and then accelerate.

The two pairs at Anzalduas State Park gave at least 73 trills or series of trills in 11½ hours. Often it appeared to be in greeting, as when one bird joined its mate at the nest (11 times) or elsewhere (8 times). It was used when the pair approached the nest (11 times) or swam away from it (11 times). It seemed to function also as a triumph note, as after an aggressive encounter with a Pied-billed Grebe (4 times) or with another pair of Least Grebes (3 times). In this context it was very similar to

the triumph duets of the Horned Grebe (Storer, 1969) and also to that triggering the more complex patter ceremonies of the New Zealand Dabchick (Storer, 1971). In three instances, trills by the Least Grebes followed my disturbing the birds. Four times when I could not see the birds, one pair responded in kind when the other pair trilled, and in four others, trills followed aggressive notes. When trills were used as a greeting, more frequently (19 out of 23 times) the male swam up to the female. These observations suggest that the call is important in reinforcing the pair bond and in announcing or maintaining territory, somewhat as song serves this purpose in many passerines.

This call has apparently been reported by several authors. Gross (1949) refers to a "prolonged rapidly-uttered, rattle-like call" and a "trill," both given by the male. Palmer (1962) lists a "trill," and Slud (1964) calls it "a kind of watery churr or shushing whinney." Zimmerman (1957) in describing a rushing display reported that "one bird uttered a high-pitched, nasal *nye, nye, nye, nye.*" This might have been the trill or an otherwise undescribed note.

Contact notes.—A soft note, which I have transcribed as "gup," is frequently given by both members of the pair in the vicinity of the nest. I heard it given by birds coming to, at, or on the nest (24 times), during inviting (4 times) and building (once), and as the mates approached each other (3 times) away from the nest. As the mate approaches, a bird may switch from advertising to contact notes; and, conversely, when a distant mate does not respond to contact notes a bird may switch to advertising. One or both birds may use contact notes as they swim together before trilling. The use of contact notes in these situations and the softness of these notes suggest that their use is associated with low-intensity situations. This note is evidently the "low short note used during copulation and sometimes between pair at nest" (Palmer, 1962) and also the "series of faint notes" which the male gave as he approached the nest containing newly hatched young (Gross, 1949).

Aggressive call.—A high-pitched nasal note, which I transcribed as "anh," is often given singly or in series in the course of aggressive encounters. I heard it on at least six occasions. Once I was able to determine that it was the male which gave the call. At other times the birds were too far away or out of sight behind vegetation. The call was given while birds flew toward (unseen) antagonists and during actual territorial fights and was followed by trilling as fighting birds returned to their mates. I have not been able to equate this with other notes described in the literature.

RELATIONSHIPS

The Least Grebe belongs to a group of species which can be characterized by having downy young with one or more patches of rufous down on the crown (Storer, 1967). This includes the species listed by Peters (1931) in the genera *Polioccephalus* and *Podilymbus*. For purposes of discussion here, these species can best be combined into four subgroups, each consisting of forms which comprise a superspecies or group of closely related species. These subgroups center around the species *podiceps* (with *gigas*), *ruficollis* (with *novaehollandiae*, *rufolavatus*, and *pelzelinii*), *dominicus*, and *poliocephalus* (with *rufopectus*). The relationships of *dominicus* have been unclear (Storer, 1963b), but sufficient new evidence has accumulated to merit a reassessment of its systematic position. This will be done by first presenting an arrangement based on morphological characters, and then by testing this arrangement with information based on behavior.

The birds in the *podiceps*, *ruficollis*, and *dominicus* subgroups share many similarities. In winter plumage, all have white underparts and throats, dark caps, and light brownish cheeks. In the breeding season, the underparts become heavily mottled with blackish, the throat black, and the cheeks and neck gray (*podiceps*, *dominicus*), rufous (*ruficollis*), or black (*gigas*). The *podiceps* subgroup differs from

the other two (and from all other grebes) in several ways: The ulnar origin of *M. extensor longus digiti II* is not confined to the extreme proximal end of the bone and the distal head of *M. extensor longus digiti III* is absent (Sanders, 1967); the bill is short, deep, powerful, and strongly pried in the breeding season; and the feathers of the lores, forehead, and malar region have broad, flattened tips to the rachis (Stettenheim, 1974). I consider these character states all to be advanced over those in the other three subgroups.

Members of the *ruficollis* subgroup (except *pelzelinii*) are advanced over the presumed common ancestor of the group in having an expanded, yellow-green gape and rufous on the cheeks and nape. The *dominicus* and *poliocephalus* subgroups are advanced in lacking the canal in the hypotarsus for the tendon of *M. flexor perforatus digiti II* (Storer, 1963b) and in having conspicuously light (ivory to orange-yellow) eyes in the breeding season. Members of the *poliocephalus* subgroup differ from all the others in having the throat and cheeks the same dark color, white, hair-like nuptial plumes on the head, and the chest rusty; and they lack mottling on the underparts.

On the basis of this morphological evidence, the *podiceps* subgroup forms one distinct assemblage, the genus *Podilymbus*; the *poliocephalus* subgroup forms another, for which the generic name *Poliocephalus* is available. The Least Grebe differs from the *ruficollis* subgroup in the hypotarsal character and in details of the breeding plumage and soft parts, but in general is closest to that subgroup. I would therefore consider the two subgroups to comprise the genus *Tachybaptus*.

These relationships are supported by some of the behavioral evidence which is available. Based on data from *rufopectus* (Storer, 1971), the *poliocephalus* subgroup is the most distinct, having unique diving and pattering displays and lacking trills. In this emphasis on visual rather than vocal displays, as in plumage characters, the *poliocephalus* subgroup may be considered convergent with the genus *Podiceps sensu stricto*, from which it differs markedly in the pattern of the downy young, courtship behavior, and type of head plumes. The species of *Podilymbus* differ from the others in having a sexually dimorphic "song" and a pivoting display. The Least Grebe resembles the members of the *ruficollis* subgroup, as far as known, in its vocal repertoire and its peculiar, presumably cryptic, resting posture; but it differs from the latter in its soliciting posture and postcopulatory displays (cf. Bandorf, 1970). The Least Grebe has presumably been isolated from its Old World relatives for a long time, and the differences between it and members of the *ruficollis* subgroup might be sufficient to place it in a separate subgenus for which the name *Limnodytes* (Obserholser, 1974) is available. However, as the number of species is small, this seems impractical.

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APPENDIX

Stomach contents of Least Grebes

RWD 14681, adult male, La Avellana, Dept. Sta Rosa, Guatemala, 10 April 1973. Stomach contents: 1 dermestid beetle, 1 probably terrestrial beetle, 2 or 3 probable true bugs, upwards of 50 ants, fish bones, many feathers.

RWD 14690, adult female, 4 mi. SW of La Avellana, 28 April 1973. Stomach contents: 2 bugs, 3 beetles (at least 2 scarabids), 5 ants, fish bones, many feathers.

RWD 14691, adult female, same locality and date. Stomach contents: about 30 shrimp, 1 crab, 5 bugs, 2 beetles, 4 flies, 13 ants, few feathers.

RWD 14999, adult male, La Avellana, Dept. Sta Rosa, Guatemala, 2 May 1974. Stomach contents: 122 ants, few feathers (most or all in pyloric plug).

RWD 15034, adult male, 6 km NW of Garita Chapina, Dept. Juliata, Guatemala, 5 May 1974. Stomach contents: 2 dragonflies, probably Libellulidae, 1 water boatman nymph, 8 hydrophilid beetles, 1 beetle, probably a weevil, 12 ants, some winged, 2 nematodes, probably parasitic, few feathers (most or all in pyloric plug).

RWD 14527, adult male, 42 miles south of Tecolutla, Veracruz, Mexico, 31 March 1973. Stomach contents: 3-4 water striders, 1 probable backswimmer, 3-4 probable gyrinid beetles, 1 scarabid, 1 weevil, 6 ants, 6 large, hairy spiders, a few probable fish ribs, few feathers (most or all in pyloric plug).

RWD 14766, first-year female, 7 miles east of Río San Pedro y Pablo, Campeche, Mexico, 2 April 1973. Stomach contents: 2 crayfish, 4 bugs (including 1 giant water bug), 2 beetles (including 1 weevil), 1 ant, moderate number of feathers.

RWD 14767, first-year male, same locality and date. Stomach contents: 2 large shrimp, 1 beetle, few feathers.

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